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Integrated taxonomy, biology and biogeography of the Afrotropical genus *Xyloctonus* (Coleoptera, Curculionidae, Scolytinae)

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Abstract

The peculiar Afrotropical bark beetle genus *Xyloctonus* Eichhoff, 1872 is revised and its biology described. Several unusual morphological features reflect adaptations to predator avoidance as they are highly exposed during mating externally on tree trunks and branches. Observations invariably indicate that males and females abandon the nest under bark at an early stage of progeny, the males already before eggs hatch, potentially engaging in subsequent additional matings. Most species have a clear preference for host plants in the plant family Sapotaceae. Although the genus is broadly distributed in forested parts of Africa, Madagascar and Mauritius, most species are found in the eastern part of this range. A Bayesian biogeographical analysis revealed a possible origin of the genus in Madagascar in the early Eocene, with subsequent colonisation of the southern African region in late Eocene. This contrasts with the closely-related xyloctonine genus *Ctonoxylon* Hagedorn, 1910, which is of western Congolian ancestry and more recently reached Madagascar multiple times during late Miocene. Two new species are described: *Xyloctonus magnus* **sp. nov.** from Madagascar and *X. genieri* **sp. nov.** from Burkina Faso. Synonyms are proposed for *X. subcostatus* Eggers, 1939 (= *X. striatus* Eggers, 1939) and *X. scolytoides* Eichhoff, 1872 (= *X. latus* Eggers, 1922). Identification to species is provided in a key illustrated with photographs of most species.

Key Words

bark beetles, Bayesian Binary MCMC, phylogeny, Reconstruct Ancestral State in Phylogenies, taxonomy

Introduction

Xyloctonini are a characteristic group of tropical bark beetles in the weevil subfamily Scolytinae. It includes five genera: *Glostatus* Schedl, 1939, *Cryphalomimus* Eggers, 1927, *Ctonoxylon* Hagedorn, 1910 and *Xyloctonus* Eichhoff, 1872 are all Afrotropical, whereas *Scolytomimus* Blandford, 1895 is restricted to the Indo-Malayan and Australian Regions. A recent revision of *Glostatus* placed this genus in a separate subtribe Glostatina Jordal, 2023 and also revealed a rather chaotic taxonomy for this group of beetles. *Ctonoxylon* and *Xyloctonus* are, on the other hand, taxonomically stable groups at the generic level and their morphology leaves little doubt about their affinity (Jordal 2023). The peculiar look of *Xyloctonus* (Figs 1, 2) and the other genera in subtribe Xyloctonina is most strikingly expressed in the rounded and inflated shape of the pronotum, a deep groove on the anterior side of the protibiae and the impressed lateral sclerites of the metathorax for reception of femur and tibiae (Menier 1974). Such highly-specialised features led some authors to place these weird beetles in their own subfamily Xyloctoninae (Hopkins 1915; Schedl 1961b) or family Xyloctonidae (Eichhoff 1878). Observations on their biology are few and anecdotal, but all species are true bark beetles with likely narrow host plant preferences (Schedl 1961b).

Both *Ctonoxylon* and *Xyloctonus* are broadly Afrotropical. However, *Xyloctonus* has one-third of the species endemic to Madagascar, whereas *Ctonoxylon* until recently did not have any species verified from this island (Wood and Bright 1992). The predominantly Congolian affinities of *Ctonoxylon* may explain its scarce presence on Madagascar, whereas the largely Zambesian distribution of African *Xyloctonus* could have facilitated a closer

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connection with this island. A biogeographical analysis of Xyloctonini and outgroups is, therefore, presented to test these hypotheses, using reconstruction of ancestral areas in a Bayesian framework.

Rather few publications have dealt with the taxonomy of *Xyloctonus* (see Eggers (1939); Schedl (1953); Menier (1974)) and, generally, very little is known about morphological variation, behaviour and geographical distribution. The taxonomy and biology are, therefore, revised, including an identification key and photographic illustrations. Two new species are described and two other species synonymised which leaves the total number of species at 15 (Table 1). Recent fieldwork has provided new host and country records which, together with observations on their behaviour, will contribute to a better understanding of distribution and ecology.

Table 1. Currently valid species of the genus *Xyloctonus* Eichhoff, 1872 and their known distribution.

Xyloctonus aethiops Schedl, 1953	Madagascar
Xyloctonus bimarginatus Eggers, 1939	Democratic Republic of the Congo
Xyloctonus biseriatus Schedl, 1953	Madagascar
Xyloctonus genieri Jordal, sp. nov.	Burkina Faso
Xyloctonus maculatus Schedl, 1965	South Africa
Xyloctonus magnus Jordal, sp. nov.	Madagascar
Xyloctonus mauritianus Menier, 1974	Mauritius
Xyloctonus niger Schedl, 1938	Uganda
Xyloctonus opacus Schedl, 1957	Rwuanda
Xyloctonus pubifer Schedl, 1965	Zambia, South Africa
Xyloctonus punctipennis Eggers, 1939	Somalia
Xyloctonus quadricinctus Schedl, 1941	Ghana, Tanzania
Xyloctonus quadridens Schedl, 1953	Madagascar
Xyloctonus scolytoides Eichhoff, 1872	Tropical Africa, incl. South Africa
Xyloctonus subcostatus Eggers, 1939	Guinea, Burkina Faso, Democratic Republic of the Congo, Sudan, Tanzania, Mozambique

Material and methods

Eggers (1939) often used the informal term type and cotype. The purpose of these terms was clearly holotype (see Wood and Bright (1992)) and paratype. Specimens studied are deposited in the following museum collections:

CAS California Academy of Sciences, San Francisco, USA.
CMNC Canadian Museum for Nature, Ottawa, Canada (Genier coll).
RBINS Royal Belgian Institute of Natural Sciences, Brussels, Belgium.
RMCA Musee Royal de l'Afrique Centrale, Tervuren, Belgium.
MNHN Museum National d'Histoire et Naturelle, Paris, France.
MZH Finnish Museum of Natural History, Helsinki, Finland.
NHMUK The Natural History Museum, London, UK.
NHMW Naturhistorisches Museum, Vienna, Austria.
USNM National Muséum of Natural History, Washington D.C., USA.
UWCP Museum of Natural History, University of Wroclaw (Wanat coll).
ZMHB Museum für Naturkunde der Humboldt-Universität, Berlin, Germany.
ZMUB University Museum of Bergen, Norway.

Specimens collected by the author were dissected from recently dead wood and lianas identified by local plant experts. Careful removal of bark allows for reconstruction of family structures and brood size. It was noted if a nuptial chamber was present inside the entrance and whether the direction of the egg tunnel (gallery) was parallel or transverse to the wood grain as this is often a species specific trait. The stage of development (larvae, pupae, teneral adults) was noted for each observation and if one or both parents were still present.

External morphological characters were studied in a Leica MZ16 and photographs made with Leica LAS software on a Leica M205 C stereomicroscope. Internal morphological characters were dissected and reported in a previous paper (Jordal 2023).

Biogeographical analyses were based on a new time-calibrated phylogenetic tree as the basis for reconstructing ancestral areas. The molecular data used to reconstruct the time tree were mitochondrial COI and nuclear 28S and EF-1α, as described in a recent publication (Jordal 2023). Approximate clade ages were estimated in Beast 1.10.4 (Drummond and Rambaut 2007), with the xml file prepared in Beauti. Rates were calibrated with time estimates from a previous analysis of Scolytinae, based on 18 genes (Pistone et al. 2018) and given a normal distribution with five standard deviations to accommodate for uncertainties in these estimates. Nodes used for calibration included the root which combined taxa from Ipini, Hypoborini and Micracidini at 88 Ma, Micracidini without *Leiomicracis* at 79 Ma and the Neotropical micracidine clade at 65 Ma. These particular nodes had relatively small differences between stem and crown ages and estimates were robust across different studies (Jordal and Cognato 2012; Pistone et al. 2018; Jordal 2021a, b). Published estimates on the Xyloctonini lineages were excluded to avoid potential bias in the new estimate using a much larger ingroup sample.

Ancestral areas were reconstructed in RASP (Yu et al. 2020) using 1 million iterations of the Bayesian Binary MCMC (BBM) method, based on the new time-tree reconstructed in Beast. The preferred model F81 allows different frequencies of areas in the dataset which better accommodate the small samples of species from Madagascar and southern Africa compared to the Congolian and Zambesian regions. Due to the highly-restricted distribution of most species of Xyloctonini, the maximum number of occupied areas was set to 2. Areas were generally defined as the biogeographic regions (realms) of the

world, with the target area Afrotropics (Ethiopian region) divided further into statistically-defined regions *sensu* Linder et al. (2012): Madagascar, Congolian (= Shaba, Congolian and Guinean clusters), Zambesian and southern African (= Namib, Kalahari, Cape and Natal clusters) regions, which are the only relevant areas for the Xyloctonini taxa treated here.

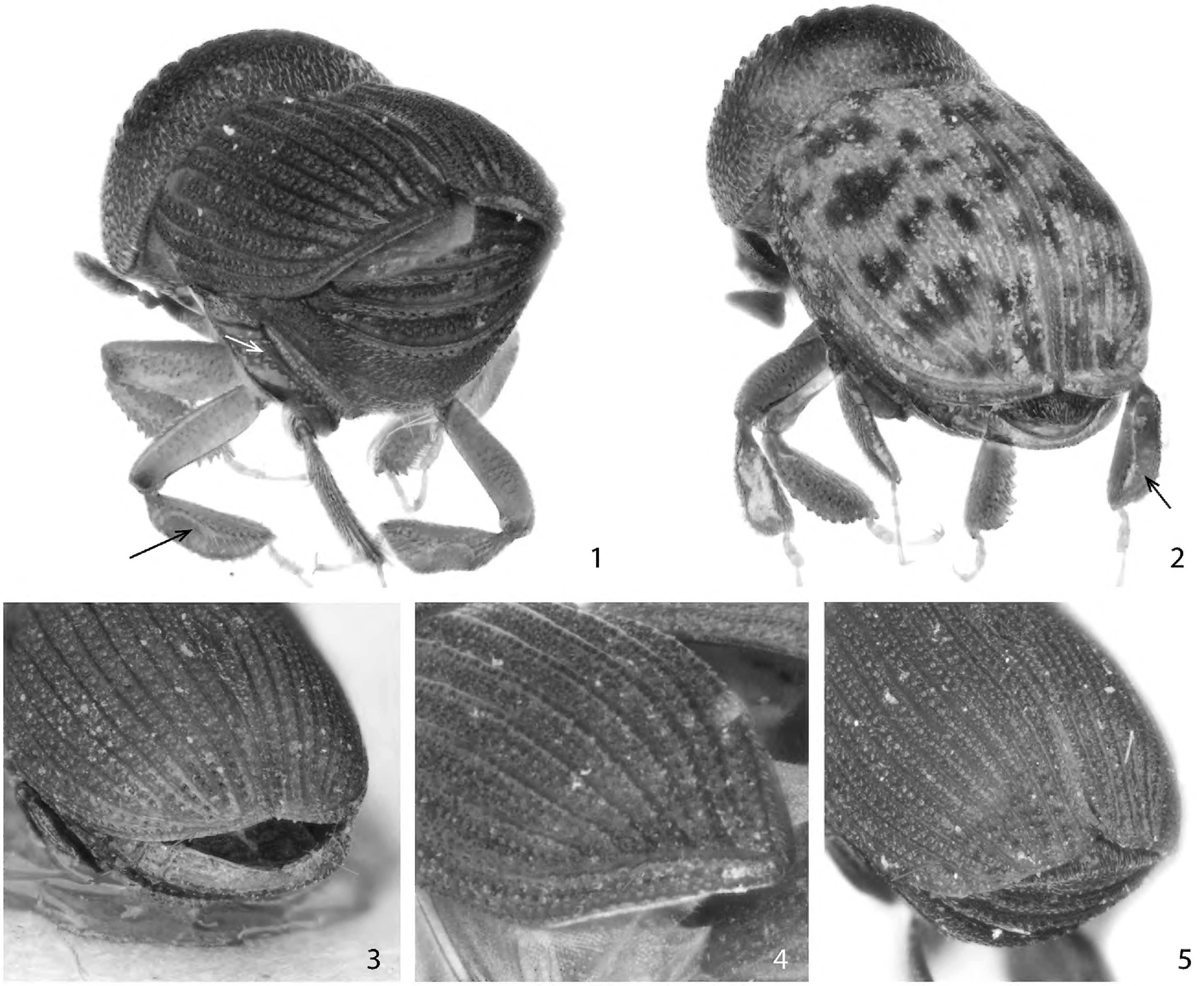
Results

Phylogenetics and Afrotropical biogeography of Xyloctonini

The recent phylogenetic study of Xyloctonini resulted in a monophyletic group of five *Xyloctonus* species which were maximally supported as sister to *Scolytomimus* Blandford 1895 (fig. 1 in Jordal (2023)). The distinctness of *Xyloctonus* is also supported morphologically (fig. 2 in Jordal (2023)), in particular by the symmetrically rounded and flat antennal club with two or three procurved sutures and the genus connects with *Scolytomimus* by the steeply rising venter meeting a short elytral declivity (Figs 1, 2). These two genera share with *Cryphalomimus* a carinated shape of the elytral interstriae (Figs 1–5) and, together with *Ctonoxylon*, all four genera have deeply-grooved protibiae for reception of the tarsi and a large and scoop-like manubrium of the aedeagal tegmen (Jordal 2023).

A new Beast analysis of the molecular data showed similar relationships between genera (Fig. 6), with *Glostatus* separated from the other four genera. Within *Xyloctonus* the two South African taxa *X. maculatus* and *X. latus* were nested within the Malagasy clade, as opposed to the previously published MrBayes analysis (fig. 1 in Jordal (2023)).

Reconstructions of possible ancestral areas revealed contrasting patterns for the three xyloctonine genera with multiple species sampled (Fig. 6). On the basis of



Figures 1–5. Posterior view of elytral declivity in **1.** *Xyloctonus quadridens*; **2.** *X. maculatus*; **3.** *X. subcostatus* (paratype of *X. striatus*); **4.** *X. pubifer*; **5.** *X. scolytoides* (paralectotype of *X. latus*). Black arrows points at the shallow furrow on the posterior side of the metatibiae, similar to mesotibiae. White arrow points to the impression of the metaventrite which receives the metafemur. Yellow arrows point at elytral interstriae 9, which in Figs 1–4 runs to the elytral sutures and blocks interstriae 1–8 from reaching elytral apex; in *X. scolytoides* (Fig. 5) all interstriae reach the posterior margin of the elytra.

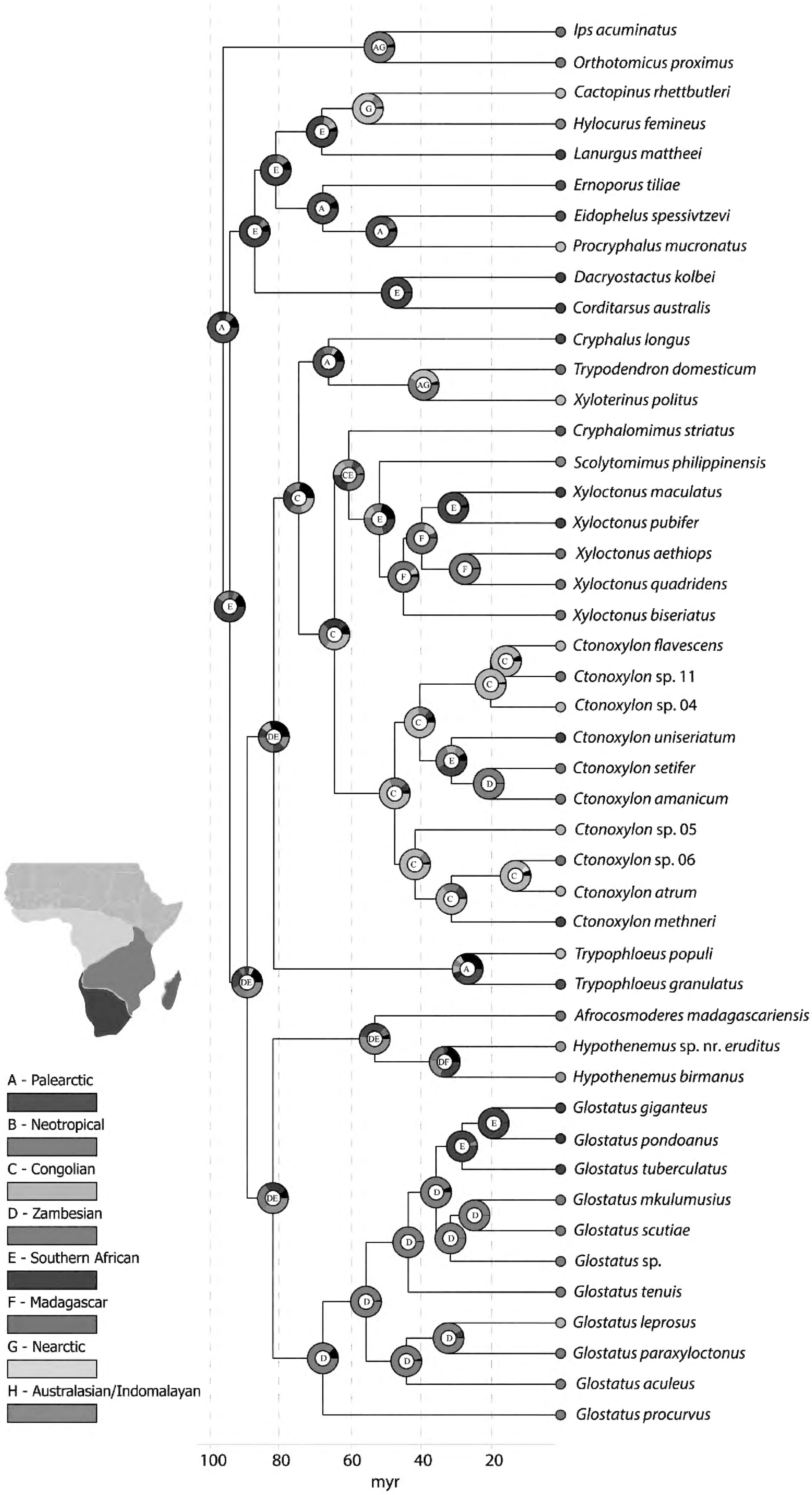


Figure 6. Reconstruction of ancestral geographic areas in RASP using the BBM method on a Beast estimated time-tree. The most likely ancestral area is noted by a letter in centre of each pie diagram, with alternative states coloured according to their likelihood proportions. The map inserted shows the approximate extent of relevant Afrotropical subregions *sensu* Linder et al. (2012).

this dataset, *Xyloctonus* was inferred to have originated in Madagascar 52–45 Ma. The southern region of Africa was thereafter reached from Madagascar no later than 31 Ma. *Ctonoxylon* indicated a Congolian ancestry some 64–47 Ma, with more recent expansions to the Zambesian and southern African regions. Colonisation of Madagascar occurred twice and no earlier than 13 and 16 Ma, possibly much later, as these were single species with rather similar morphology to their continental sister species (Jordal, in prep.). *Glostatus* is not part of the core Xyloctonini and is not found on Madagascar (Jordal 2023); its inferred ancestry in the Zambesian region was strongly supported and occurred some 82–68 Ma, with a more recent expansion to the southern parts of Africa not earlier than 35 Ma.

Taxonomy

Xyloctonus Eichhoff, 1872

Type species. *Xyloctonus scolytoides* Eichhoff, 1872 (by monotypy).

Diagnosis. Eyes divided, except broadly emarginated in *X. maculatus* and *X. genieri* sp. nov. Antennal scapus longer than the 6-segmented funiculus; club flat, outline round, with three, or more rarely two, strongly procurved sutures marked by dense white or golden setae (Figs 22, 40). Pronotum spherical in both lateral and frontal view, lateral margins carinate; anterior half asperate, with either two or four raised teeth along anterior margin. Scutellar shield (scutellum) slightly detached from elytra; interstriae carinate (only declivity in *X. aethiops*), interstrial carinae either reaching posterior margin or more often disrupted by a curved interstriae 9 that reaches elytral suture near apex; declivity short and gently sloping (steep and longer in *X. maculatus*). Metanepisternum, metaventrite and first ventrite usually with split setae, trifid or occasionally plumose setae often present near mesoventrite. Ventrites 3–5 usually steeply rising to meet elytra. Procoxae contiguous; protibiae with deep furrow of anterior face to receive tarsi; other tibiae with distinct, but shallower furrow on its posterior face. Proventriculus with posterior plate strongly reduced, anterior plate with partially open and indistinct median suture, plate covered by simple obtuse tubercles. Male genitalia with large complex intromittent organ (basal sclerites), apophyses (penis apodemes) as long as penis body; tegmen open dorsally, ventrally with a large scoop-shaped manubrium; spiculum gastrale as simple thin curved rod.

Differential diagnosis. This genus differs from *Scolytomimus* by the distinct procurved sutures in the antennal club and by the irregular impression around the scutellar shield. It is further distinguished from *Cryphalomimus* and *Ctonoxylon* by the 6-segmented antennal funicle, a rather short, oblique elytral declivity and the symmetrically procurved sutures in the antennal club.

The *emarginatus* group

Two species are included in this group, defined by having all interstriae reaching the apical margin of the elytra (Fig. 5). One of the taxon names used in the past was '*emarginatus*', now a synonym of *scolytoides*, describing this condition (see *bimarginatus* group below).

Xyloctonus scolytoides Eichhoff, 1872

Figs 7, 8, 10, 11, 13, 14

Xyloctonus scolytoides Eichhoff 1872: 134.
Xyloctonus emarginatus Eggers, 1939: 16, synonymy by Menier, 1974.
Xyloctonus latus Eggers, 1939: 14, syn. nov.

Type material. ***Syntypes*** of *X. scolytoides*: [South Africa] Port Natal [-29.87, 30.97], Dej. [RBINS]. ***Paratype*** of *X. emarginatus*: [Democratic Republic of the] Congo, Ituri, Djugu, 13.VIII.1931, leg. J. Lebrune [RMCA]. Lectotype of *X. latus*: [Ethiopia] Abyssinia, 8000 feet alt. IX–X 1926, Dr. H. Scott [NHMUK]; and paralectotype, same data [NHMW].

Diagnosis. Length 2.1–2.6 mm, 1.9–2.1× as long as wide, colour light to very dark brown; antennal club with two visible procurved sutures; frons with fine setae; anterior margin of pronotum with two raised teeth (Figs 7, 10); all elytral interstriae carinate, reaching posterior elytral margin; strial and interstrial punctures moderately deep; scutellar shield impressed in middle, appearing bilobed; elytral suture with bulgy locking mechanism behind scutellar shield; setae on lateral metaventrite mainly bifid or trifid, anteriorly more plumose.

Distribution. Burkina Faso (new country record), Ghana, Ivory Coast, Nigeria, Cameroon, Democratic Republic of the Congo, Uganda, Sudan, Ethiopia, Tanzania, Zambia, South Africa.

New records. Burkina Faso, Bale, Boromo [11.755, -2.929], 250 m alt. F. Genier, leg., 10.8.2006, light trap; Comoe, Foret de Boulon [10.343, -4.510], 270 m alt., F. Genier leg., 9.7.2006, flight intercept trap, light trap and Malaise trap; Kompienga, 15 km E Nadiagou [11.113, 0.909], 155 m alt., F. Genier leg., 25.8.2005, flight intercept trap, light trap and Malaise trap; Loroum, Toulfe [13.873, -1.950], 300 m alt., F. Genier leg., 16.7.2006, light trap; Nahouri, Foret de Nazinga [11.045, -1.420], 310 m alt., F. Genier leg., 27.7.2006, light trap and Malaise trap; Passore, 8 km SE Yako [12.928, -2.216], 320 m alt., F. Genier leg., 7. 8. 2006, light trap; Sanguie, Foret de Sorobouli [11.893, -2.799], 270 m alt., F. Genier leg., 13.7.2005 and 28.7.2006, light trap; Ouagadougou, 03.11.1973, R. Linnavouri [MZH]; Bobo Dioulasso, 03.11.1973, R. Linnavouri [MZH]; Nigeria, Kano-Wudil, 17.05.1973, R. Linnavouri [MZH]; Serti [7.51, 11.36], 29. March 1970, coll. J.T. Medler; Cameroon, 35 km S Garoua [9.01, 13.34], 30 March 1972, at black light, JA Gruwell; Tanzania, W. Usambara, Kwai, 1600 m, P. Weiss [ZMHB]; South Africa,

Mpumalanga, Telperion Reserve, 1450 m alt. [-25.735, 28.985], 08.12.2019, beating, M. Wanat leg. [1, UWCP]; Gauteng, Pretoria, Wapadrand, 1540 m alt. [-25.847, 28.384], 09.12.2019, beating, M. Wanat leg. [1, UWCP].

Biology. This species is the only species in the genus that is frequently and broadly collected. It is found feeding and breeding in many host plants, such as *Butyrospermum parkii*, *Madhuca latifolia*, *Mimusops caffra* (all in Sapotaceae), *Olea capensis* (Oleaceae), *Garcinia* (Clusiaceae) and *Acacia* (Fabaceae) (see Schedl (1961b)). It is notable that the majority of records are from Sapotaceae which is by far the most typical host plant family for the genus.

Comments. The lectotype of *X. latus* is identical, except for some of the setae on upper lateral part of the metaventrite which tend to be trifid or pentafid over a larger area rather than the typical trifid setae in the *X. scolytoides* types.

Xyloctonus niger Schedl, 1938

Figs 9, 12, 15

Xyloctonus niger Schedl, 1938 d: 452.

Type material. ***Syntypes***: Uganda, Entebbe [0.04, 32.42], 11-II-1938, P. Chandler [NHMUK, NHMW].

Diagnosis. Length 2.5 mm, 2.1× as long as wide, colour black, shiny; antennal club with two visible procurved sutures; frons glabrous; anterior margin of pronotum with two raised teeth clearly longer than broad; all elytral interstriae carinate to posterior elytral margin; strial and interstrial punctures very shallow making walls of carinae rather smooth and shiny; scutellar shield a rounded button, clearly detached from the surrounding elytra; elytral suture with bulgy locking mechanism behind scutellar shield; setae on lateral metaventrite bifid.

Distribution. Uganda.

Biology. Known from the two collections in Uganda; the non-type series were dissected from *Tabernaemontana holzkii* (Apocynaceae) (see Menier (1974)).

Comments. This species is very similar to *X. scolytoides*, but can be distinguished by the smooth and shiny interstrial carinae which is not indented along the carina wall, the glabrous frons and the consistently bifid setae on the lateral part of the metaventrite.

The *bimarginatus* group

All species (except *X. opacus* and *X. punctatus*) have interstriae 9 curved and continued to the elytral suture such that none of the interstriae 1–8 reaches the apical margin (Figs 1–4); thereof the name '*bimarginatus*'. In the two deviant species, the gap between the ninth interstriae and the apical margin nearest apex is so tight that interstriae 1–3 apparently reach the apical margin (Fig. 20). Nine species have exactly two raised teeth at the anterior margin of the pronotum, whereas another group of six species have four raised teeth along the anterior margin of the pronotum.

Species with two-spined pronotum

Xyloctonus opacus Schedl, 1957

Figs 16, 19, 22

Xyloctonus opacus Schedl, 1957: 43.

Type material. ***Holotype***: Ruanda [Rwanda], Ihembe, 29-VIII-1952, Dr. Schedl [RMCA].

Diagnosis. Length 1.9–2.1 mm, 1.9–2.0× as long as wide, colour black, dull; antennal club with one visible procurved suture; frons finely pubescent; anterior margin of pronotum with two raised teeth; elytral interstriae 1–3 continue to posterior elytral margin, interstriae 4–8 terminate in the transverse interstriae 9 that merge with apical margin at level of interstriae 3; scutellar shield rough, weakly impressed in middle; elytral suture straight (mesal locking mechanism normal).

Distribution. Rwanda.

Previous reports from Madagascar (Schedl 1977) are *X. biseriatus* [NHMW].

Biology. Collected from *Chrysophyllum* (Sapotaceae) branches about 2–8 cm in diameter (Schedl 1961b). Egg tunnels were cut transversely to the grain and the number of larvae ranged between 14 and 44 (n = 4).

Xyloctonus punctipennis Eggers, 1939

Figs 17, 20, 23

Xyloctonus punctipennis Eggers, 1939: 16.

Type material. ***Holotype***: Somalia, Basso Ganana [-0.6, 41.7], VII–VIII-93, V. Bottago [USNM].

Diagnosis. Length 1.8–2.4 mm, 2.0–2.1× as long as wide, colour brown, shiny; antennal club with two visible procurved sutures; frons with scant fine setae; anterior margin of pronotum with two raised teeth; elytral interstriae 1–3 continue to posterior elytral margin, interstriae 4–8 terminate in the transversely curved interstriae 9 that merge with the apical margin at level of interstriae 3; scutellar shield smooth, weakly impressed in middle; elytral suture with bulgy locking mechanism near scutellar shield.

Distribution. Somalia.

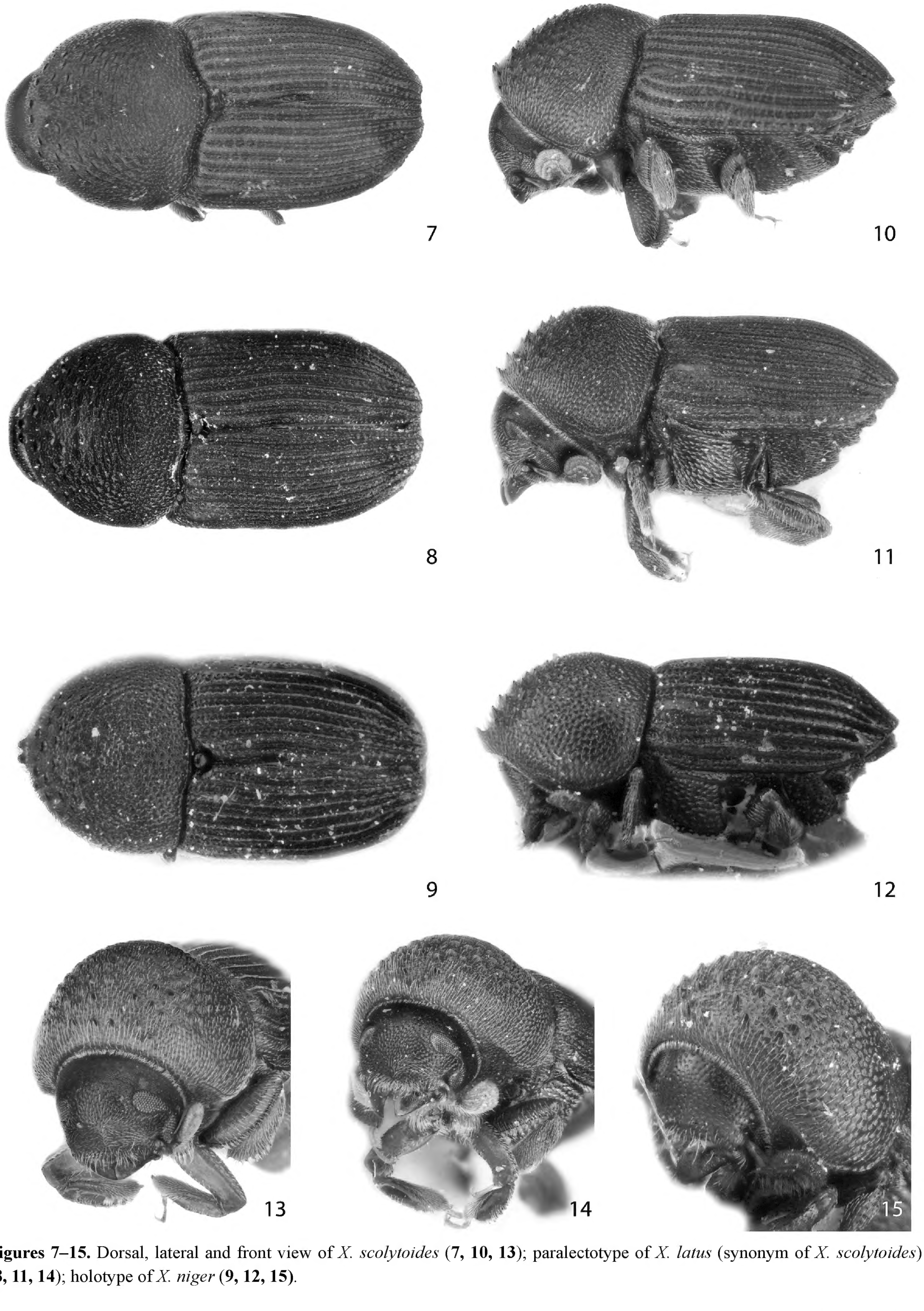
Xyloctonus biseriatus Schedl, 1953

Figs 18, 21, 24

Xyloctonus biseriatus Schedl, 1953: 76.

Type material. ***Lectotype***: Madagascar, Region de l'Androy Ambovombe, Dr J. Decorse, 1901, 1 au 15 dec, 00 [MNHN]. ***Paralectotype***: Madagascar sud, Fort Dauphin, Allaud, 1900 – I [MNHN].

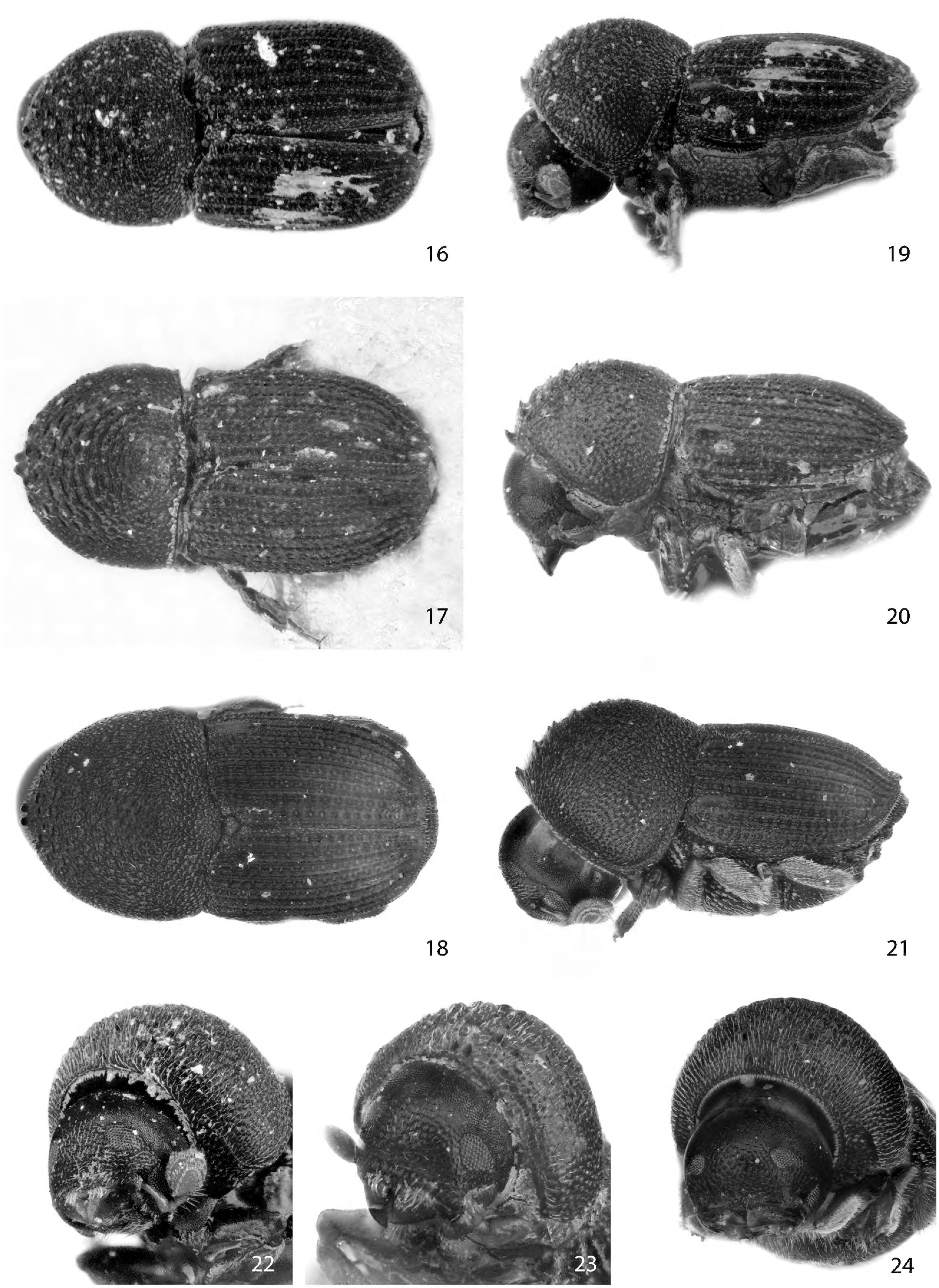
Diagnosis. Length 1.5–2.0 mm, 1.8–1.9× as long as wide, colour black, dull; antennal club with two visible procurved sutures; frons glabrous; anterior margin



Figures 7–15. Dorsal, lateral and front view of *X. scolytoides* (**7, 10, 13**); paralectotype of *X. latus* (synonym of *X. scolytoides*) (**8, 11, 14**); holotype of *X. niger* (**9, 12, 15**).

of pronotum with two raised teeth; elytral interstriae 9 curves before apex and continues transversely to elytral suture; spaces between strial punctures with elongate elevation that mimics a dashed line; scutellar shield slightly impressed in middle; elytral suture straight.

Distribution. Madagascar.



Figures 16–24. Dorsal, lateral and front view of holotype of *X. opacus* (**16, 19, 22**); paratype of *X. punctipennis* (**17, 20, 23**); *X. biseriatus* (**18, 21, 24**).

New records. Madagascar, Ankarafantsika NP [-16.264, 46.828], 200 m alt. ex. *Diospyros* branch, 8 May 2015, B. Jordal, leg. [ZMUB]; Reserve speciale de l'Ankarana, 22.9 km SW Anivorano [-12.93, 49.16], B. Fischer [CAS].

Biology. Previously collected in dry forests in the south of Madagascar and the new record from further north was also from a dry forest type. Specimens were collected twice from thin branches of *Diospyros* (Ebenaceae), about 3 cm in diameter. The egg tunnel was cut in the phloem and inner bark layers, transverse to the grain of wood. About 30–40 young tenerals and larvae were produced per brood (Table 2). Parents were not present at late larval stage. Colonisation densities were high, with only an average of 0.5 cm distance between egg tunnels.

Xyloctonus pubifer Schedl, 1965

Figs 25, 28, 31

Xyloctonus pubifer Schedl, 1965a: 365.

Type material. ***Holotype*:** South Africa, Port Elisabeth [-33.76, 25.45] [NHMW].

Diagnosis. Length 2.8–2.9 mm, 1.8–1.9× as long as wide, colour dark brown; frons finely pubescent; anterior margin of pronotum with two tiny, raised teeth; elytra with dense, fine micro-setae, interstrial and strial punctures dense and similarly sized; elytral interstriae 9 curves before apex and continues to elytral suture; scutellar shield impressed in middle, bilobed, with bifid, short setae; elytral suture straight.

Distribution, South Africa, Zambia.

New records. South Africa, Western Cape Province, Natures Valley [-33.965, 23.562], 8 Nov. 2007, ex. *Sideroxylon inerme*, B. Jordal, leg. [ZMUB]; Eastern Cape Province, Van Stadens Resort, beating 18.11.2013, M. Wanat leg. [UWCP].

Biology. Collected multiple times in this study, from the bark layer of *Sideroxylon inerme* (Sapotaceae). Females were found alone with larvae, the male was not observed, but presumably left their progeny at an earlier stage as observed in other species of the genus. Brood production ranged from 20–27 (n = 3). Flight times were observed in July and August in Zambia (Beaver and Löyttyniemi 1985) and estimated to be early October in South Africa, based on expected developing time for the larvae collected in this study.

Xyloctonus mauritianus Menier, 1974

Xyloctonus mauritianus Menier, 1974: 662.

Type material. ***Holotype***, male: Mauritius, Corps de garde [-20.26, 57.45], 20. V. 1934, J. Vinson [MNHN].

Diagnosis. Length 2.1–2.3 mm, 1.9× as long as wide, colour brown, elytra maculated; antennal club with one clearly visible and one faint procurved suture; anterior margin of pronotum with two raised teeth; scutellar shield impressed in middle, with two bulbs at anterior corners; elytral interstriae 9 curves before apex and continues to elytral suture; elytral suture straight.

Distribution. Mauritius.

Xyloctonus subcostatus Eggers, 1939

Figs 26, 27, 29, 30, 32, 33

Xyloctonus subcostatus Eggers, 1939: 15.
Xyloctonus striatus Eggers, 1939: 18, syn. nov.

Type material. ***Holotype*:** Deutsch Ost Afrika [Tanzania], Bez. Tabora, Ngulu [-3.72, 32.46], vi. 1911, sammler W. Methner [USNM]. ***Paratypes*** of *X. striatus*: Mozambique, Sangadzé, Moulima [-17.4, 35.0], sur *Acacia*, 1928, P. Lesne [MNHN, NHMW].

Diagnosis. Length 1.7–2.8 mm, 2.0× as long as wide, colour brown; antennal club with two visible procurved sutures; male vertex with a simple pars stridens (Fig. 32); anterior margin of pronotum with two raised teeth; pronotum slightly narrower than elytra; elytral interstriae 9 curves above the posterior margin of elytra and continues to elytral suture; interstriae lightly punctured; scutellar shield broad, slightly impressed in middle, roughly punctured; elytral suture with bulgy locking mechanism; setae on lateral upper part of metaventrite bifid.

Distribution. Mozambique, Tanzania, Sudan, Democratic Republic of the Congo (new country record) Guinea, Burkina Faso (new country record).

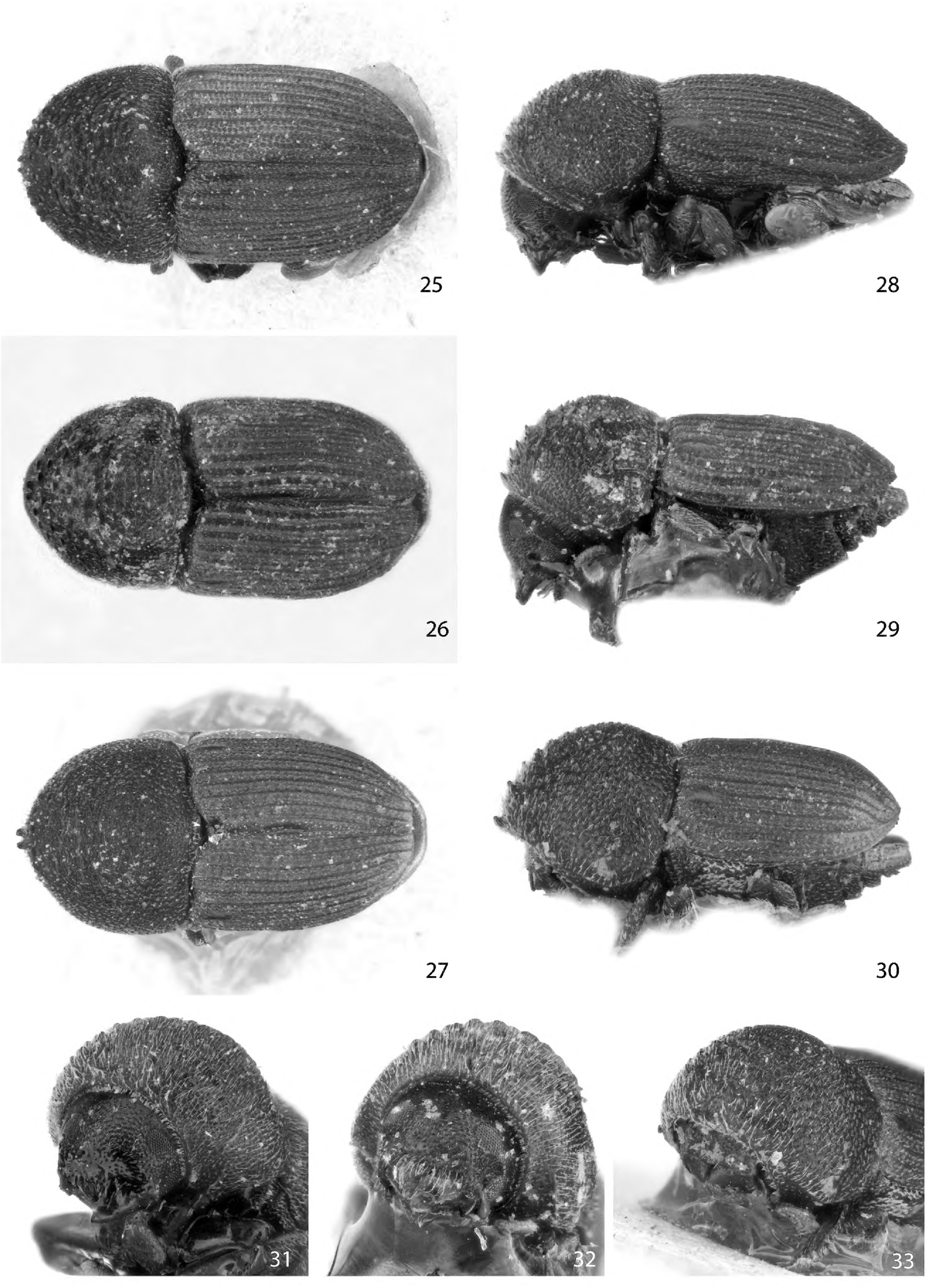
New records. Burkina Faso, Comoe, Foret de Boulon, 270 m alt., 10.343, -4.510, 9.7.2006, F. Genier leg. [2, Genier coll.]; Democratic Republic of the Congo, Moba, 780 m alt., -7.030, 29.763, 01.10.1953, H. Bomans leg. [1, RMCA].

A specimen from the Democratic Republic of Congo [RMCA] was erroneously identified by Schedl as *X. scolytoides*.

Biology. Collected from an *Acacia* (Fabaceae) branch (identified as *X. striatus*). Two males were collected by a

Table 2. Summary of reproduction in species of *Xyloctonus* published in: (1) this paper; (2) Schedl (1977); (3) Schedl (1961b).

Species	Host family	Diam. (cm)	Egg tunnel direction	Brood size	male leave	female leave
Xyloctonus aethiops[1,2]	Phyllanthaceae	1–4	longitudinal	21–40	egg	larvae
Xyloctonus biseriatus[1]	Ebenaceae	2–4	transverse	30–40	egg or larvae	larvae
Xyloctonus pubifer[1]	Sapotaceae	10–20	transverse	20–27	egg	pupae
Xyloctonus maculatus[1]	Sapotaceae	10–20	transverse	12–21	egg	larvae
Xyloctonus opacus[3]	Sapotaceae	5–14	transverse	14–41	?	larvae
Xyloctonus quadridens[1]	Sapotaceae	1–20	transverse	30–50	?	?



Figures 25–33. Dorsal, lateral and front view of holotype of *X. pubifer* (**25, 28, 31**); paratype of *X. subcostatus* (**26, 29, 32**); paratype of *X. striatus* (synonym of *X. subcostatus*) (**27, 30, 33**).

Malaise trap in Burkina Faso, in a dry bushland. The records from south-eastern parts of the Democratic Republic of the Congo, Sudan and Guinea are also from very dry forests below 1000 m altitude. Although present on one of Eggers 'co-types' (paratypes), the male pars stridens is here reported for the first time.

Comments. Paratypes ('co-types') of *X. striatus* are identical to *X. subcostatus*, except elytral interstriae 9 is a little less separated from the elytral apex.

Xyloctonus bimarginatus Eggers, 1939

Figs 34, 37, 40

Xyloctonus bimarginatus Eggers, 1939: 17.

Type material. ***Holotype*:** [Democratic Republic of the] Congo, Kundelungu [-10.25, 27.60], leg. Mme Tinaut [RMCA].

Diagnosis. Length 2.2–2.6 mm, 1.9–2.0× as long as wide, colour brown, shiny; antennal club with two clearly-visible procurved sutures, a third and fainter suture near the margin; frons with scant fine setae, vertex in males with pars stridens; anterior margin of pronotum with two raised teeth; elytral interstriae 9 curves before apex and continues to elytral suture, in dorsal view apical margin of elytra extending beyond margin of interstriae 9, finely serrated; scutellar shield impressed in middle, bilobed; elytral suture with bulgy locking mechanism.

Distribution. Democratic Republic of the Congo.

Comments. Only known from the type. It is not unlikely that *X. subcostatus* is the same species. However, the type differs by having a longer flange at the elytral apex, in dorsal view extending beyond interstriae 9. It also has coarser punctures along the wall of the interstrial carinae.

Species with four-spined pronotum

Xyloctonus maculatus Schedl, 1965

Figs 35, 38, 41

Xyloctonus maculatus Schedl, 1965b: 113.

Type material. ***Paratype*:** South Africa, Cape Province, Port Elisabeth [-33.7, 25.6], VIII. 1960, ex *Sideroxylon inerme*, leg. J.S. Taylor [NHMW].

Diagnosis. Length 1.7–2.2 mm, 2.1–2.2× as long as wide, colour light to dark brown, with small, dark spots on elytra; antennal club with two visible procurved sutures; eyes not divided, but deeply emarginated; anterior margin of pronotum with four raised teeth, median pair longest; elytral interstriae 9 curves before apex and continues to elytral suture; scutellar shield rounded, with two tiny pits at anterior corners; elytral suture straight; elytral declivity long, nearly vertical; venter nearly straight.

Distribution. South Africa.

New records. South Africa, Western Cape Province, Natures Valley [-33.965, 23.562], 8 Nov. 2007, ex *Sideroxylon inerme*, B. Jordal, leg. [ZMUB].

Biology. Exclusively recorded from *Sideroxylon inerme* (Sapotaceae). Fallen trees were crowded with males running on the surface in search of females sitting in newly-excavated tunnel openings. Mating occurred at the entrance with only the posterior part of the female exposed. There was no nuptial chamber. Egg galleries were dense and males were guarding the entrance as long as the female was accessible.

Xyloctonus genieri sp. nov.

https://zoobank.org/0977F970-815A-409A-B00F-94EDD3140070

Figs 36, 39, 42

Type material. ***Holotype*:** Burkina Faso, Comoe, Foret de Boulon [10.343, -4.510], 270 m alt., F. Genier leg., 10.7.2006, in Malaise trap [CMNC].

Diagnosis. Eyes emarginated, not divided. Antennal club with one faint procurved suture. Anterior margin of pronotum with four equally-sized, raised teeth.

Description. Length 1.6 mm, 2.1× as long as wide; colour black. **Frons** convex, transversely impressed just above epistoma, surface finely rugose, vestiture scant. Eyes deeply sinuate, broadly emarginated. Antennal funiculus 6-segmented, club finely pubescent, basal suture procurved, others not visible. **Pronotum** coarsely asperate on anterior two-thirds, asperities transversely elongated; anterior margin with four raised teeth. **Scutellar shield** subquadrate, with four small tubercles. **Elytral** striae reticulated, punctures shallow, irregular; interstriae carinated throughout; interstriae 9 reaching elytral suture; elytral suture straight. **Metaventrite** and nearby sclerites and ventrite I with bifid setae.

Distribution and biology. Only known from the type locality in a very dry bushland, collected in a Malaise trap.

Etymology. Named after the coleopterist François Génier who collected the type specimen in Burkina Faso.

Xyloctonus aethiops Schedl, 1953

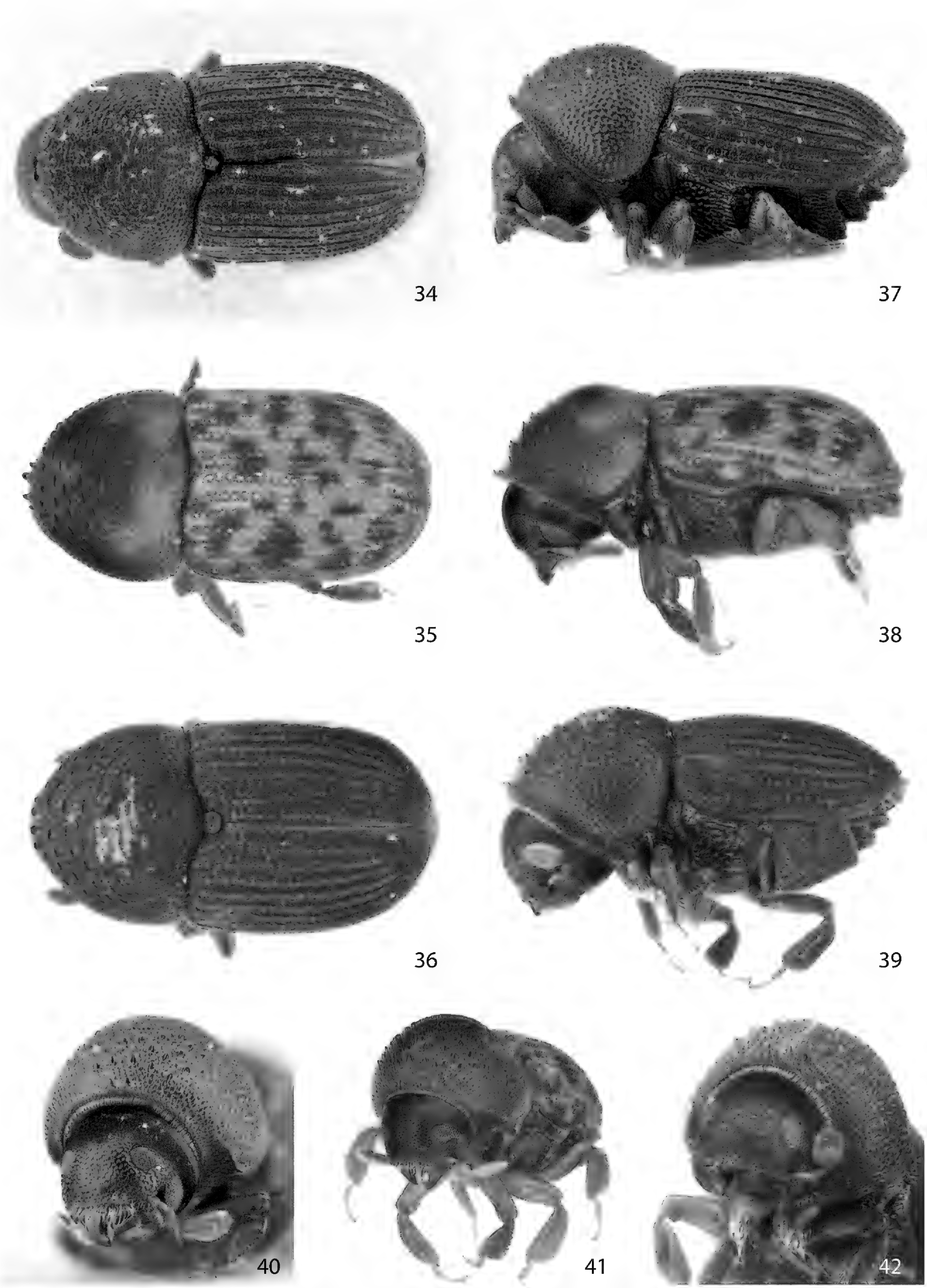
Figs 43, 45, 47, 48

Xyloctonus aethiops Schedl, 1953: 77.

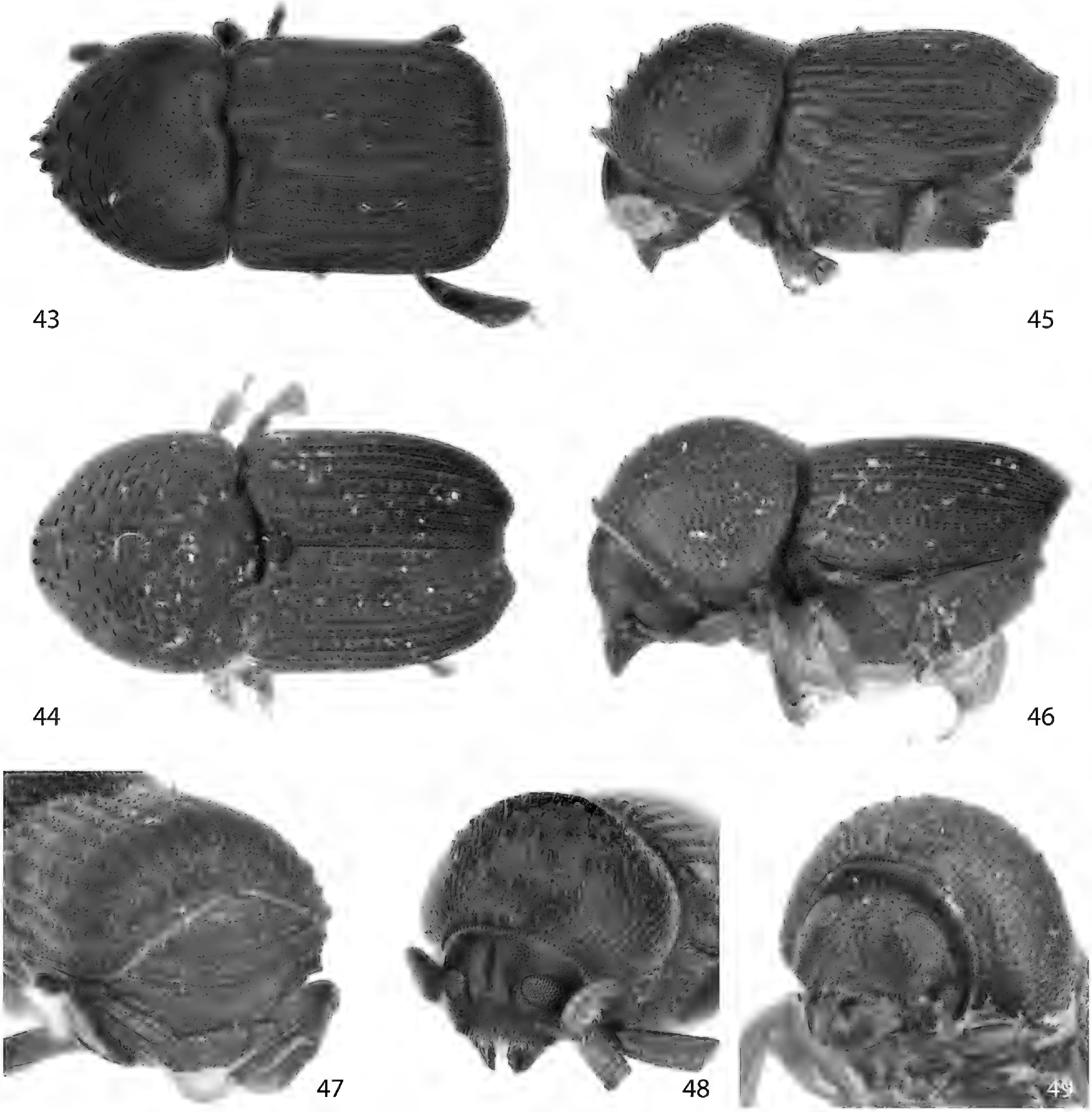
Xyloctonus stenographus Schedl, 1961a, synonymy by Menier (1974).

Type material. ***Lectotype***, *X. aethiops*: Madagascar, Ankorika [-12.24, 49.36], K. E. Schedl, 1951 [MNHN]. ***Holotype*** of *X. stenographus*: Madagascar, Perinet [-18.93, 48.41], 28. XI. 1952, Dr. K. E. Schedl [MNHN].

Diagnosis. Length 1.3–1.6 mm, 2.0× as long as wide, colour dark brown; vertex with faint (false) pars stridens; antennal club with two visible procurved sutures; anterior margin of pronotum with four raised teeth, median teeth longest; elytral interstriae 9 curves before apex and continues to elytral suture; elytral



Figures 34–42. Dorsal, lateral and front view of *X. bimarginatus* (**34, 37, 40**); *X. maculatus* (**35, 38, 41**); *X. genieri*, holotype (**36, 39, 42**).



Figures 43–49. Dorsal, lateral and front view declivity and venter with strong spines, of *X. aethiops* (**43, 45, 47, 48**); *X. quadricinctus*, holotype (**44, 46, 49**).

interstriae elevated, flattened, carinated on and near declivity only; scutellar shield transversely oval; elytral suture straight. Ventrite I swollen on median third of its posterior margin, ventrite II with four spines along the posterior margin.

Distribution. Madagascar.

New record. Madagascar, Andasibe, Mantadia National Park [-18.861, 48.447], 900 m alt. 15 May 2015, ex *Uapaca* twig, B. Jordal, leg. [ZMUB].

Biology. Two collections from known host were both in the same plant family Phyllanthaceae: *Wielandia mimosoides* (originally in *Savia*) (Schedl 1977)) and *Uapaca* sp. This is the only *Xyloctonus* that cut their egg tunnels parallel to the grain of the wood. Three broods with larvae were dissected from a thin twig of 1 cm thickness and were without parents present. Brood size ranged between 21 and 28 (n = 3).

Xyloctonus quadricinctus Schedl, 1941

Figs 44, 46, 49

Xyloctonus quadricinctus Schedl, 1941: 387.

Type material. ***Holotype*:** [Tanzania] Usambara, Derema 850 m alt., 7.10.1891, Conradt S. [NHMW].

Diagnosis. Length 2.1 mm, 2.0× as long as wide, colour dark brown; antennal club with three visible procurved sutures; anterior margin of pronotum with four equally-long raised teeth; elytral interstriae 9 curves before apex and continues to elytral suture; scutellar shield rounded, tuberculate; elytral suture straight.

Distribution. Ghana, Nigeria, Tanzania.

Biology. It has been collected from a Sapotaceae tree, *Gambeya albida* in Ghana (see Schedl (1961b)). Nothing else is known about its biology.

Xyloctonus quadridens Schedl, 1953

Figs 50, 52, 54

Xyloctonus quadridens Schedl, 1953: 77.

Type material. ***Syntypes*:** Madagascar, Mt. D'Ambre, 1930, Sicard leg. [MNHN].

Diagnosis. Length 1.9–2.2 mm, 1.8–1.9× as long as wide, colour black, dull; antennal club with two visible procurved sutures, a third suture intergrades with the apical margin of club; anterior margin of pronotum with four raised teeth; elytral interstriae 9 curves before apex and continues to elytral suture; scutellar shield rugose, slightly impressed in middle; elytral suture straight; male profemur with tiny spine on its ventral side.

Distribution. Madagascar.

New records. Madagascar, Andasibe, Mantadia National Park [-18.861, 48.447], 900 m alt. 15 and 16 May 2015, ex *Labramia bojeri* log, B. Jordal, leg. [ZMUB]; Reserve speciale de l'Ankarana, 22.9 km SW Anivorano, B. Fischer [CAS].

Biology. The collection from *Labramia bojeri* (Sapotaceae) is the first known host for this species. Egg tunnels were cut transversely to the grain. Broods were old and only fully sclerotised adults were found. Counts of larval mines ranged between 30 and 50 (n = 4).

Comments. According to Menier (1974), the male should have a pars stridens on its vertex. However, none of the males at hand had this feature, despite the unique presence of a femoral spine (n = 4).

Xyloctonus magnus sp. nov.

https://zoobank.org/55896893-5EB7-41E2-A7B8-6F301C1E18C8

Figs 51, 53, 55

Type material. ***Holotype*:** Madagascar, Anjozorobe 11 km SE [-18.43, 47.94], Malaise trap, BLF2375, B. Fischer, leg. [CAS].

Diagnosis. Largest species in the genus, 3.4 mm long; scutellar shield longitudinally elongated as a heart-shaped scoop; sutural side of interstriae 1 with dense fine trifid setae.

Description. Length 3.4 mm, 1.9× as long as wide, colour dark brown. **Frons** impressed just above epistoma, nearly glabrous. Antennal club with one strongly procurved suture, others faint; funiculus 6-segmented. Upper and lower eye parts widely separated, roughly punctured between. **Pronotum** very broad, broader than elytra; anterior margin with four raised teeth, median pair slightly longer, asperities near summit as fine granules, intermixed with shiny punctures. **Scutellar shield** elongated, densely pilose, narrowly impressed to form a heart-shaped scoop. **Elytral** striae with transversely elongated punctures, spaced by longitudinally raised ridges, the whole stria appearing as a dashed line. Elytral interstriae 9 curves before apex and continues to elytral suture; elytral suture straight. **Metaventrite** and surrounding sclerites, including ventrite I, with mainly trifid setae.

Distribution. Madagascar.

Biology. One specimen was taken in a Malaise trap.

Etymology. Based on the Latin masculine adjective *magnus*, meaning large, referring to the body size of the species.

Identification key to the species of *Xyloctonus*

1 Elytral interstriae 9 terminates near lateral margin, interstriae 1–8 all reaching apical margin (Fig. 5) 2
– Interstriae 9 reaching at least to interstriae 3, usually to the elytral suture, cutting off interstriae 1–8 which do not reach apical margin (Figs 3, 4) 3
2 Frons glabrous; pronotal teeth at the anterior margin longer than broad; elytral carinae smooth and shiny; punctures very shallow; colour shiny black (Uganda) .... *X. niger*
– Frons finely pubescent; pronotal teeth at anterior margin as long as broad; elytral interstriae with fine short setae on each side of deeply-punctured interstrial carinae; strial punctures deep; colour matt brown to dark brown (Afrotropical) .... *X. scolytoides*
3 Anterior margin of pronotum with four raised teeth (Figs 35, 36) 4
– Anterior margin with two raised teeth (Figs 16–18) 9
4 Eyes sinuate, not divided (Figs 41, 42) 5
– Eyes completely divided, sometimes with a line of scattered ommatidia partly connecting them 6
5 Elytra lightly coloured with dark spots; declivity steeply sloping (South Africa) .... *X. maculatus*
– Elytra uniformly dark; declivity gently sloping (Burkina Faso) .... *X. genieri* sp. nov.
6 Elytral interstriae on disc flattened, carinate near elytral apex; ventrite II with four spines along the posterior margin; body length < 1.7 mm (Madagascar) .... *X. aethiops*
– Interstriae sharply carinate throughout; posterior margin of ventrites without longer spines; body size > 1.8 mm 7

7 Pronotal teeth along anterior margin spaced by more than width of a tooth (Fig. 44); elytral apex more broadly and deeply attenuated, apical tip of each elytron positioned between interstriae 3 and 4 (Ghana, Tanzania)............... *X. quadricinctus*

– Pronotal teeth at margin nearly contiguous (Figs 50, 51); elytral apex shallowly attenuated with tip of each elytron positioned between interstriae 2 and 3... 8

8 Large species, length 3.4 mm; epistomal hair-like setae prominent, pointing forwards; scutellar shield longer than broad; ventral sclerites with mainly trifid setae (Madagascar) .... *X. magnus* sp. nov.

– Smaller, length < 2.4 mm; epistomal hair largely recumbent, pointing downwards; scutellar shield broader than long; ventral sclerites with mainly bifid setae (Madagascar)...*X. quadridens*

9 Elytral interstriae 9 discontinued at the level of interstriae 3, interstriae 1–3 continue to apical margin.................... 10

– Elytral interstriae 9 continues to interstria 1 with a clear gap between interstriae 9 and apical margin, all interstriae 1–8 discontinued before apical margin... 11

10 Elytra appearing shiny; elytral suture with bulgy locking mechanism near scutellar shield (Fig. 17) (Somalia)............... .... *X. punctipennis*

– Elytra appearing dull, reticulate, particularly inside punctures; elytral suture straight throughout (Fig. 16) (Rwanda).... ....*X. opacus*

11 Elytral striae with longitudinal tubercle between transversely oval punctures which appears like a straight dashed line (Madagascar)..*X. biseriatus*

– Elytral striae with round punctures, without the dashed line pattern... 12

12 Elytral suture straight; pronotal asperities near summit as broad irregular ridges; interstriae with fine setae on each side of the interstrial carina 13

– Elytral suture with bulgy locking mechanism, pronotal asperities not much broader than tall; interstrial setae barely visible... 14

13 Pronotal teeth at anterior margin longer than broad, strial punctures large, in a single row; body length 2.0–2.2 mm (Mauritius)...*X. mauritianus*

– Pronotal teeth at margin not longer than broad; strial punctures small, in two confused rows; body length > 2.7 mm (South Africa, Zambia) ....*X. pubifer*

14 Apical rim of elytra extends far beyond the transverse interstriae 9, forming a lip (Figs 34, 37) (Democratic Republic of the Congo) ....*X. bimarginatus*

– Elytral interstriae 9 near elytral apex approximately at the same level as elytral apex (Burkina Faso and Guinea to Sudan, south-eastern Democratic Republic of the Congo, Mozambique, Tanzania)...*X. subcostatus*

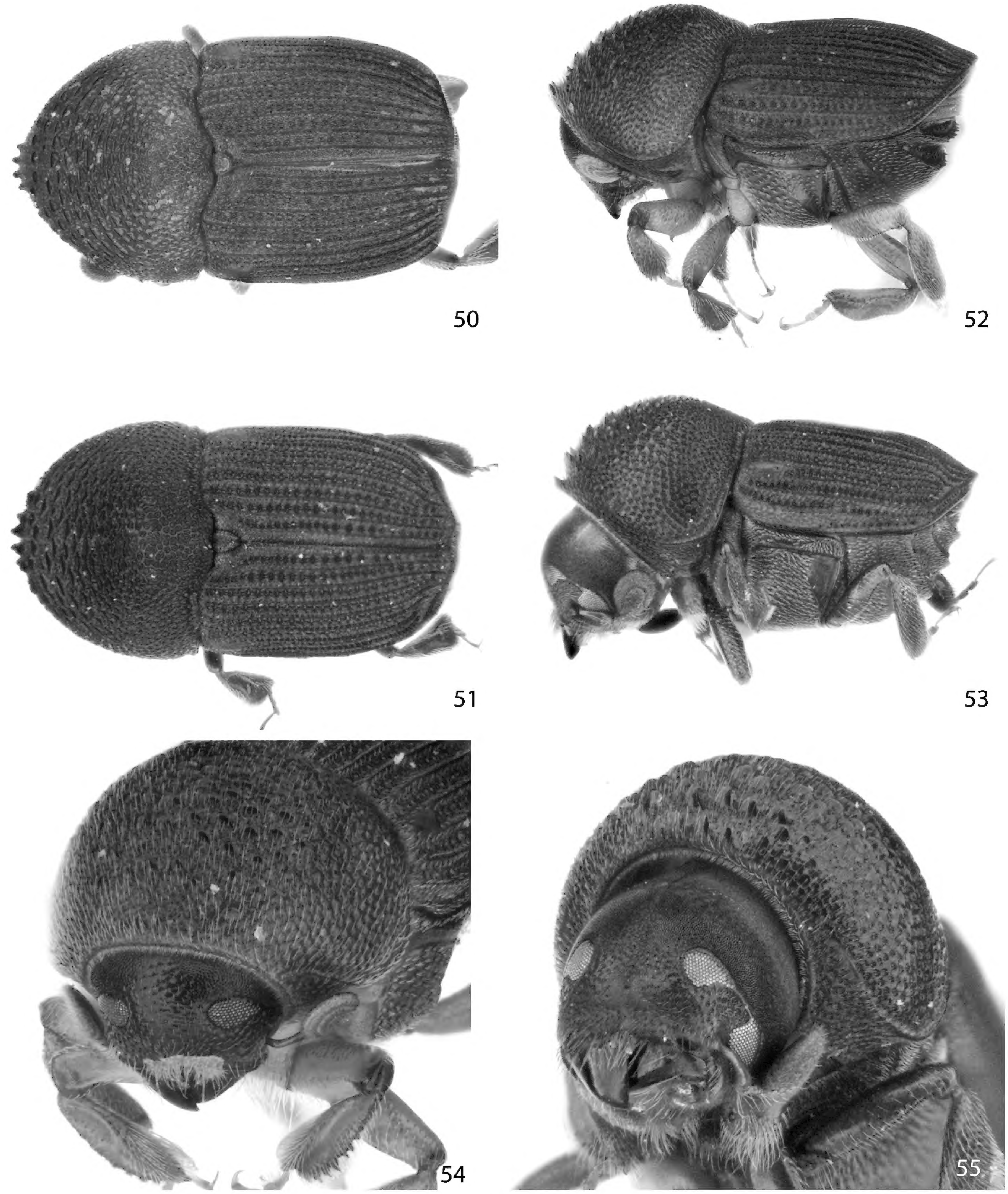
Discussion

Biology

Xyloctonus species are easily recognised by their compact morphology which reflects a likely adaptation to avoid predators. When disturbed, they easily fall off the branch or trunk after retracting their tarsi into deep grooves on their tibiae, particularly the protibiae. The legs are, furthermore, strongly flattened and the metatibiae and femur fit into a depression of the metanepisternum and metaventrite, which is carinated along its front edge. Observing their mating behaviour in the field reveals fast running of males on the bark to find a colonising female, with which he mates in the tunnel opening. He will, thereafter, guard the opening to prevent further access to the female by other males. This is a very exposed situation that increases the risk of being taken by predatory insects such as ants or even by insectivore birds. These beetles have an impressive reaction speed and fall off the log extremely quickly. Species in *Xyloctonus* and other Xyloctonina are, therefore, amongst the most specialised with morphologies deviant from the average bark beetle body shape (Schedl 1961b).

Both males and females stay only for a short time with their broods (Table 2). Males usually leave before the eggs are hatching and females at some undetermined time later, but usually well before the young tenerals appear. The rather aggressive mating behaviour observed in males of several species seems connected to the external location of mating which involves a high risk of predation. It is likely that the early escape from the egg gallery provides further opportunities for mating and perhaps compensates for the high predation risk during mate search. This behaviour was most clearly demonstrated by *X. maculatus* which may establish a new nest on the same log. Limited parental care with the potential for multiple matings is perhaps also motivated by the generally low brood sizes compared to the average for bark beetles (Browne 1961), although low brood size could also be a consequence of limited parental care.

The low number of known host plants, restricted to a handful of plant families, indicates a high level of host specialisation in this genus. Six of the ten species with known host records were taken from plants in Sapotaceae. Mono- and oligophagy are typical for bark beetles as opposed to the broader range of host plants used by ambrosia beetles (Beaver 1979; Hulcr et al. 2007). The few host plants recorded are not a serendipitous artefact from rare collecting events as multiple collections over time and from localities far from each other were from the same host (Schedl 1957, 1961b, 1977; this study). Five of



Figures 50–55. Dorsal, lateral and front view of male *X. quadridens* (**50, 52, 54**); *X. magnus*, holotype (**51, 53, 55**).

the six species reported in this study were collected multiple times in one field work session, suggesting that these species are not extremely rare, although *X. scolytoides* is the only one collected more than four times.

Plastic dimorphism

A stridulatory apparatus is sometimes present, but varies in size and distinctness. Menier (1974) reported the presence of a stridulatory file in the upper frons of male *X. quadridens*, which was not observed in the new material. The males of this species have a spine on the ventral side of the femur, but, nevertheless, there was no pars stridens present in any of the new specimens collected. Multiple series of *X. subcostatus* also indicated that at least some males exhibit a pars stridens, previously not reported. Somewhat intermediate is *X. aethiops* which has a partially developed and likely a false pars stridens, a feature not seen in the type material of this species. One should not

exclude the possibility that cryptic species may exist and which differ in their stridulatory apparatus. However, such crypsis seems less likely given their otherwise identical morphology. To firmly conclude on these matters, DNA from multiple populations is needed to test this hypothesis.

Biogeography

Restricted use of host plants is associated with limited geographical distributions and high endemism in nearly all species of *Xyloctonus*. Amongst the 15 currently-recognised species, only four have a broad distribution including two or more biogeographical regions. However, only one of these have trustworthy records from both western and eastern to southern parts of Africa. The core distribution is in the Zambesian region and four species are found endemic to Madagascar and one on Mauritius. Unfortunately, many of the older samples from the Zambesian region were unsuitable for DNA sequencing and, therefore, limited the biogeographical inference in the BBM analysis. It was, nevertheless, clear that *Xyloctonus* differs strongly from *Ctonoxylon* which unequivocally demonstrated a Congolian ancestry, with much more recent and repeated colonisations of Madagascar and the southern parts of Africa.

It is likely that broader sampling of *Xyloctonus* will further confirm a single ancient colonisation of Madagascar during the Eocene. This was a favourable time to colonise the island due to the trade winds blowing primarily in an eastern direction (Yoder and Nowak 2006; Ali and Huber 2010; Jordal 2021b; Ali and Hedges 2022), but examples of colonisations in the opposite direction are found in, for example, xyleborine (Eliassen and Jordal 2021) and micracidine beetles (Jordal 2021b). The opposite pattern is apparently the norm for *Ctonoxylon* which revealed three independent colonisations with subsequent speciation during the mid- or late Miocene. Each of the two undescribed Malagasy species and one that did not provide DNA data, are all fairly similar to, but distinct from, the African mainland sister species (unpublished manuscript). It is, therefore, possible that these have colonised Madagascar even more recently than that which the dated phylogeny indicates.

It appears more and more clear that insects are not influenced by historical trade winds to the same degree as in non-volant animals (Crottini et al. 2012; Samonds et al. 2012). On the other hand, one needs to keep in mind that most insect groups never managed to settle on Madagascar, for example, *Glostatus* which is found in rather similar ecological niches on the African continent (Jordal 2023). This genus shows a strong core distribution in the Zambesian region (see Fig. 6), with one or few dispersal events towards the southern part of Africa. This pattern is reminiscent of the one for *Ctonoxylon*, whereas *Xyloctonus* may have colonised southern Africa from Madagascar, a pattern known from several scolytine beetle groups (Jordal 2013; Eliassen and Jordal 2021; Jordal 2021b). With a steady increase in biogeographic data for Afrotropical scolytine beetles, it seems clear that patterns are variable and not particularly correlated with trade winds. A similar pattern is found in plants with windborne seeds, telling us that prevailing wind systems possibly vary more than postulated (Ali and Huber 2010; Ali and Hedges 2022).

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